



Human activities alter biogeographical patterns of reptiles on Mediterranean islands

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ABSTRACT

Aim The theory of island biogeography predicts species richness based on geographical factors that influence the extinction–colonization balance, such as area and isolation. However, human influence is the major cause of present biotic changes, and may therefore modify biogeographical patterns by increasing extinctions and colonizations. Our aim was to evaluate the effect of human activities on the species richness of reptiles on islands.

Location Islands in the Mediterranean Sea and Macaronesia.

Methods Using a large data set ($n = 212$ islands) compiled from the literature, we built spatial regression models to compare the effect of geographical (area, isolation, topography) and human (population, airports) factors on native and alien species. We also used piecewise regression to evaluate whether human activities cause deviation of the species–area relationship from the linear (on log–log axes) pattern, and path analysis to reveal the relationships among multiple potential predictors.

Results The richness of both native and alien species was best explained by models combining geographical and human factors. The richness of native species was negatively related to human influence, while that of alien species was positively related, with the overall balance being negative. In models that did not take into account human factors, the relationship between island area and species richness was not linear. Large islands hosted fewer native species than expected from a linear (on log–log axes) species–area relationship, because they were more strongly affected by human influence than were small islands. Path analysis showed that island size has a direct positive effect on reptile richness. However, area also had a positive relationship with human impact, which in turn mediated a negative effect on richness.

Main conclusion Anthropogenic factors can strongly modify the biogeographical pattern of islands, probably because they are major drivers of present-day extinctions and colonizations and can displace island biodiversity from the equilibrium points expected by theory on the basis of geographical features.

Keywords

Alien species, Anthropocene, elevation, human influence, island area, isolation, Macaronesia, Mediterranean Sea, species richness, topography.

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INTRODUCTION

MacArthur and Wilson's theory of island biogeography (MacArthur & Wilson, 1967) is one of the major theoretical foundations of biogeography and ecology (Whittaker & Fernández-Palacios, 2007). The theory of island biogeography assumes that species richness on oceanic islands depends on the equilibrium between species extinction, species colonization and

speciation. Simple geographical features, such as island size and isolation, are primary drivers of the extinction–colonization balance, thus determining the species richness of islands. Even though more complex models have been proposed, including factors such as energy availability (Wright, 1983; Kalmar & Currie, 2006), habitat heterogeneity (Diamond, 1969; Kadmon & Allouche, 2007) and disturbance (Whittaker, 1995), predictions from island biogeography models have repeatedly been confirmed

by both experimental and observational studies all over the world (Whittaker & Fernández-Palacios, 2007): area and isolation are still considered the key drivers of insular richness (e.g. Kreft *et al.*, 2008).

Habitat alteration and biological invasions are major causes of the current biodiversity crisis: human activities are thus directly responsible for most present-day extinctions, changes in community assemblies and modifications in the geographical ranges of species (Sala *et al.*, 2000; Wilson, 2002). Islands can be particularly vulnerable to human influences (Steadman, 1993; Whittaker & Fernández-Palacios, 2007). It is therefore likely that human activities are major drivers of the current extinction–colonization processes in oceanic islands. Several studies have documented biotic changes caused by humans, showing strong relationships between human activities, extinctions and the presence of alien species (Diamond, 1969; Chown *et al.*, 1998; Blackburn *et al.*, 2004; Blackburn *et al.*, 2008). However, large-scale studies are scarce, and we are far from a clear understanding of the effects of human factors on overall biogeographical patterns.

Here, we use an extensive database on reptiles in the Mediterranean Sea and Macaronesia (Fig. 1) to investigate whether anthropogenic factors can modify the biogeographical pattern of islands, and can cause a deviation of the species–area relationship from the expected linear (on log–log axes) pattern. The study area is a climatically homogeneous region, and some authors consider Macaronesia to be part of the Mediterranean area (Daget, 1977; Cox *et al.*, 2006). The islands of the Mediterranean Sea share a large proportion of reptiles with mainland Europe and Africa, but there are also several endemic species, particularly of lizards (e.g. *Algyroides fitzingeri*, *Archaeolacerta bedriagae* and *Podarcis pityusensis*). The native reptiles of Macaronesia comprise endemic species of the genera *Tarentola* and *Chalcides*, and by the endemic genus *Galliota*. Mediterranean islands have been subject to strong human influence for millennia (Blondel & Aronson, 1999), and constitute an ideal laboratory for evaluating the long-term effects of human activities on biodiversity patterns.

We tested three hypotheses describing the effect of human impact on the diversity of reptiles in Mediterranean islands. First, we evaluated whether human impact affects the biogeographical

relationship of native species, by determining a lower species richness than predicted on the basis of classical species–area relationships. Second, we evaluated whether human impact is the major determinant of the richness of alien species. Finally, we tested whether the loss of species due to humans is compensated by the gain of alien species caused by human impact (Sax *et al.*, 2002).

METHODS

Data

We used faunistic atlases and the scientific literature (Lanza & Poggesi, 1986; Castanet & Guyétant, 1989; Delaguerre & Cheylan, 1992; Pleguezuelos *et al.*, 2002; Sultana & Falzon, 2002; Anonymous, 2003; Malkmus, 2004; Sindaco *et al.*, 2006) to obtain data on the reptile species composition on 212 islands of France, Italy, Malta, Portugal, Spain and Tunisia (Fig. 1). Following the literature (Pleguezuelos *et al.*, 2002; Lever, 2003; Sindaco *et al.*, 2006), species were classified either as native or as introduced by humans. For each island we obtained the area and the maximum elevation (a surrogate of habitat heterogeneity; e.g. Kreft *et al.*, 2008) using a variety of sources, including the original references, atlases, topographical maps and geographical publications, and we measured isolation as the distance from the continent or (if appropriate) from the nearest ‘large island’ (Corsica, Sardinia or Sicily). For each island, we also obtained human population size (years 2003–07) and the presence of airports from national statistical databases, atlases and geographical publications. These two variables were used to measure the human impact on the island. We considered airport presence as a surrogate measure of the intensity of commercial and human exchanges. Sea shipping may be more important than shipping by aircraft on islands. However, since nearly all the inhabited islands have a port, its presence could not be used as an independent variable. In our analysis, we included only islands with a surface ≥ 1 ha; this approximately corresponds to the size of the smallest islands inhabited by humans; islands with this area can host large population sizes of some reptiles (e.g. Buckley & Jetz, 2007; Pérez-Mellado *et al.*, 2008).

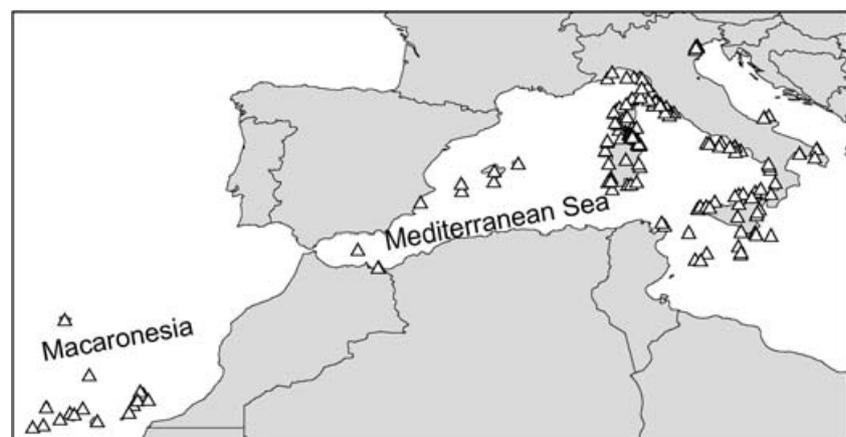


Figure 1 Study area and distribution of 212 analysed islands. Because of geographical proximity, several points are superimposed.

Statistical analyses

The variation of environmental features and that of species richness (see Fig. 2) are spatially autocorrelated, and the presence of spatial autocorrelation may bias the results of classical statistical analyses (Dormann, 2007). In preliminary analyses, the residuals of ordinary least squares regression were significantly autocorrelated, particularly at small spatial scales ($P < 0.05$ at scales up to 300 km: Fig. 2). For this reason, we analysed the data using spatial eigenvector mapping (SEVM). This is a recently developed method allowing the translation of a spatial arrangement of data points into explanatory variables capturing the spatial effects (Dormann *et al.*, 2007). In SEVM, eigenvectors reducing the spatial autocorrelation of residuals are computed and then included as spatial predictors into generalized linear models. A recent comparison among statistical methods accounting for

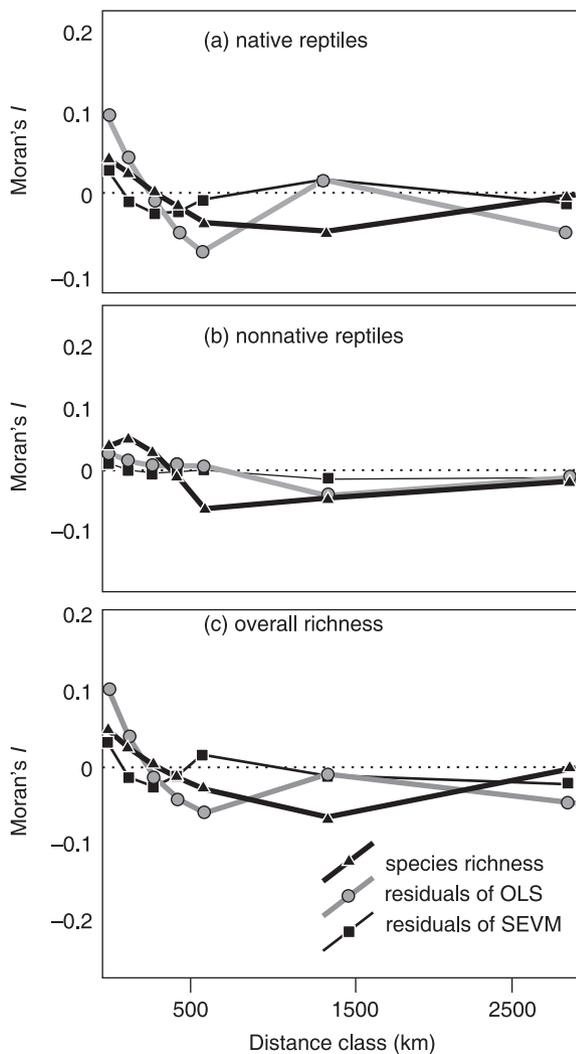


Figure 2 Moran's I correlograms for (a) richness of native reptiles; (b) richness of non-native reptiles and (c) overall richness of reptiles, measured. Bold black lines, number of species; grey lines, residuals of ordinary least squares regression (OLS); thin black lines, residuals of spatial eigenvector mapping (SEVM).

spatial autocorrelation showed that SEVM is one of the most flexible methods and is very efficient at removing residual spatial autocorrelation (Dormann *et al.*, 2007). We performed eigenvector selection following Griffith & Peres-Neto (2006). In our analyses, we carried out model selection based on the Akaike information criterion (AIC); therefore the pre-specified models (see below) were part of the eigenvector selection process. SEVM successfully removed spatial autocorrelation from the residuals of our models (Fig. 2).

We then built a series of generalized linear models including richness of native and/or introduced species as dependent variables, five explanatory variables describing island geography and human presence as independent variables and the SEVM eigenvector(s). Species richness, island area, elevation, isolation and human populations were log-transformed to improve the normality of residuals. We transformed the richness of alien species using $\log(x + 0.5)$, since in several islands there were no alien species. Species richness is a count variable, therefore Poisson models can also be appropriate. However, the results of Poisson and normally distributed models were qualitatively very similar; we therefore report the models with normal errors only.

We used a model selection approach to evaluate the support of three different models, corresponding to three potential hypotheses explaining the pattern of reptile richness. Our first model (geographical-only model) hypothesized that geographical features (area, isolation and elevation) are the major drivers of species richness; this corresponds to the classical model of island biogeography. Our second model (human-only model) hypothesized a major influence of anthropogenic factors (total human population and the presence of airports). Finally, the geographical + human model hypothesized that species richness is best explained by a combination of both geographical and anthropogenic factors. We then used the AIC to rank models according to the strength of support from the data (Burnham & Anderson, 2002). We used Akaike weights to assess the likelihood of the alternative models, and we calculated evidence ratios to compare the relative likelihood of the different hypotheses (Burnham & Anderson, 2002).

We used piecewise regression (Muggeo, 2003; Toms & Lesperance, 2003) to evaluate the presence of threshold effects in the relationship between island area and species richness. Piecewise regression allows the simultaneous evaluation of the location and the standard error of break points in generalized linear models, and an evaluation of whether the addition of such break points improves the fit of the models.

Our independent environmental variables were moderately collinear, since larger islands had higher elevations and often hosted larger human populations and airports. The strongest correlations were between area and human population ($r = 0.84$), between human population and the presence of airports ($r = 0.72$) and between area and altitude ($r = 0.71$). Hence, we calculated the variance inflation factor for all regression models. For all models and variables, the variance inflation factor was always less than 5, indicating that collinearity does not pose major problems for our models (Bowerman & O'Connell, 1990).

Due to correlation among island area, human population and the presence of airports, it is difficult to tease apart their relative effect on species richness, and therefore to evaluate whether human activities modify the relationship between species richness and area. We therefore used path analysis (Bryman & Cramer, 1990; Bollen & Long, 1993) to compare three alternative models describing the relationship between island area and native species: (m1) island size affects species richness directly and through its relationship with human impact (i.e. human impact modifies the species–area relationship); (m2) both island size and human impact affect species richness, but there is no co-action among them; (m3) island size directly affects species richness, while human impact does not have an effect. Path analysis is an extension of regression models; it allows us to provide quantitative estimates of the causal connections among variables, in relation to explicitly formulated causal models, represented in the form of path diagrams (Bryman & Cramer, 1990). We performed the analyses with R 2.5 (R Development Core Team, 2007) using the packages *spdep*, *car*, *segmented* and *sem*. We built correlograms using *sAM* 3.0 (Rangel *et al.*, 2006).

RESULTS

Richness of native species

The number of native species per island ranged from 1 to 15. The ‘geographical-only’ model explained a substantial proportion of variation ($R^2 = 0.51$) of the richness of native reptiles (Table 1). Species richness related positively to island area and elevation, and negatively to isolation. The ‘human-only’ model explained a considerably lower proportion of variation ($R^2 = 0.24$). However, the model with the highest fit was the one assuming that both geographical and human factors drove the richness of native reptiles ($R^2 = 0.59$). This geographical + human model showed an AIC value substantially lower than that for either the geographical-only or human-only model, and had an AIC weight > 0.999 (Table 1). The AIC-evidence ratio between the geographical + human and the geographical-only model was about 11 million, meaning that the geographical + human model was about 11 million times more likely to be the best model. The evidence ratio between the geographical + human and the human-only model was even larger.

According to the geographical + human model, the richness of native reptiles increases with island area and elevation, and decreases with isolation. However, when taking into account these geographical variables, species richness is lower on islands with large human populations and with airports. The slope of the species–area relationship (z) on log–log scale for the geographical-only model was 0.08 [95% confidence interval (CI) = 0.06–0.1], and was much lower than the z -value obtained when using the model that takes into account human effects (geographical + human model: $z = 0.14$, CI = 0.12–0.17).

Human and geographical variables might also show interactive effects. When we tested for two-way interactions, we found a significant interaction between distance from the continent and human population ($F_{1,202} = 12.8$, $P = 0.0004$), indicating that the

Table 1 Regression models relating richness of native reptiles to geographical and human factors.

	<i>b</i>	<i>F</i>	d.f.	<i>P</i>
Model: geographical-only				
$\Delta\text{AIC} = 32.47$; $w < 0.0001$; $R^2 = 0.512$				
Area*	0.08	61.1	1	< 0.001
Isolation*	−0.04	4.0	1	0.048
Elevation*	0.06	8.0	1	0.005
SEVM eigenvectors			3	
Residuals			205	
Model: human-only				
$\Delta\text{AIC} = 119.65$, $w < 0.0001$, $R^2 = 0.239$				
Human population*	0.05	21.7	1	< 0.001
Airport	−0.02	0.2	1	0.717
SEVM eigenvectors			3	
Residuals			206	
Model: geographical + human				
$\Delta\text{AIC} = 0$, $w > 0.999$, $R^2 = 0.589$				
Area*	0.14	105.8	1	< 0.001
Isolation*	−0.04	5.7	1	0.018
Elevation*	0.06	9.5	1	0.002
Human population*	−0.05	17.9	1	< 0.001
Airport	−0.11	4.5	1	0.036
SEVM eigenvectors			3	
Residuals			203	

b, regression coefficients; ΔAIC , difference between a candidate model and the model with the lowest Akaike information criterion (AIC); *w*, AIC weight of the model; SEVM, spatial eigenvector mapping.

*This variable was log-transformed for the analysis.

negative effect of human population was particularly strong on the most isolated islands.

If anthropogenic factors were not included in the regression model, the relationship between $\log(\text{area})$ and $\log(\text{species richness})$ was not linear. A piecewise regression with a break point (Fig. 3a) fitted the data significantly better than did a linear model ($F_{2,205} = 8.5$, $P = 0.0003$). The estimated position of the break point was $\text{area} = 1.5 \text{ km}^2$. That is, the slope of the species–area relationship changes on islands larger than 1.5 km^2 . Based on the AIC-evidence ratio, the model including a break point was 623 times more likely than the linear model. In the model including the break point, the z -value for islands with an $\text{area} < 1.5 \text{ km}^2$ was 0.15 (CI = 0.11–0.18), while it was significantly smaller for larger islands ($z = 0.04$, CI = 0.01–0.08). The break point remained significant in a model that also included isolation and elevation ($F_{2,203} = 10.5$, $P < 0.0001$).

However, if anthropogenic factors were added to the model, the piecewise regression did not converge to any break point. This strongly suggests that large islands have reduced z -values because of the negative effects of human influence. It should be noted that the break point of 1.5 km^2 corresponds to an island size above which human impact rises abruptly. In our study, only 3% of islands smaller than 1.5 km^2 had permanent inhabitants, and only one had an airport. Conversely, 80% of islands larger than 1.5 km^2 were inhabited (Fig. 3b), and 26% had an airport.

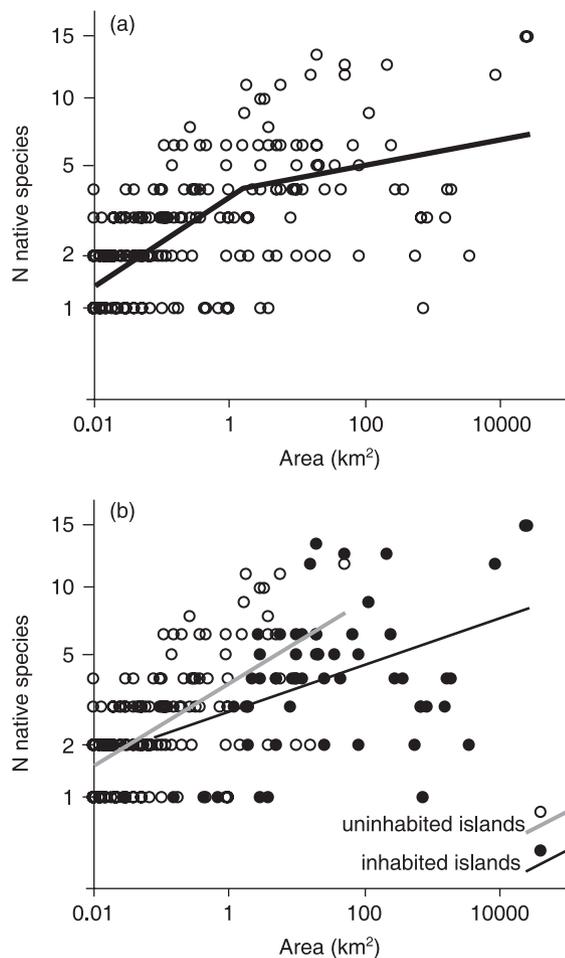


Figure 3 Relationship between island area and richness of native reptiles. (a) Piecewise linear regression, analysing all islands. (b) Linear regressions obtained analysing separately islands uninhabited (grey line, empty dots) and inhabited by humans (black line, filled dots). For uninhabited islands, $z = 0.14$; for inhabited islands, $z = 0.08$.

Inhabited islands were larger than uninhabited (t -tests: $t_{210} = 5.7$, $P < 0.0001$); similarly those with airports were larger than those without ($t_{210} = 8.7$, $P < 0.0001$). Regression lines obtained analysing separately inhabited and uninhabited islands are shown in Fig. 3(b).

Path analyses showed that the model m1 (i.e. island area affects species richness directly and through its relationship with human impact) was the best path model (Fig. 4a). Island size had a direct positive effect on reptile richness. However, area also had a positive significant relationship with human population and the presence of airports, which in turn had a negative effect on richness. Therefore, area had a negative indirect effect on richness, mediated by its relationship with human impact (Fig. 4a). Model m1 had a significantly better fit than the less complex models m2 (Fig. 4b) and m3 (Fig. 4c) (m1–m2: likelihood ratio test: $\chi^2_1 = 5.489$, $P = 0.019$; m1–m3: $\chi^2_5 = 457.87$, $P < 0.0001$). Model m2 had a significantly better fit than model m3 ($\chi^2_4 = 452.38$, $P < 0.0001$). Path coefficients were consistent with

Table 2 Regression models relating richness of non-native reptiles to geographical and human factors.

	<i>b</i>	<i>F</i>	d.f.	<i>P</i>
Model: geographical-only				
$\Delta AIC = 14.66$; $w = 0.0007$; $R^2 = 0.449$				
Area*	0.07	46.6	1	< 0.001
Isolation*	0.03	2.1	1	0.132
Elevation*	0.01	0.2	1	0.673
SEVM eigenvector			1	
Residuals			207	
Model: human-only				
$\Delta AIC = 27.53$, $w < 0.0001$, $R^2 = 0.401$				
Human population*	0.04	21.5	1	< 0.001
Airport	0.25	18.6	1	< 0.001
SEVM eigenvector			1	
Residuals			208	
Model: geographical + human				
$\Delta AIC = 0$, $w = 0.999$, $R^2 = 0.496$				
Area*	0.04	6.1	1	0.014
Isolation*	0.02	0.8	1	0.354
Elevation*	0.01	0.1	1	0.739
Human population*	0.02	1.4	1	0.223
Airport	0.19	11.5	1	< 0.001
SEVM eigenvector			1	
Residuals			205	

b, regression coefficients; ΔAIC , difference between a candidate model and the model with the lowest Akaike information criterion (AIC); *w*, AIC weight of the model; SEVM, spatial eigenvector mapping. *This variable was log-transformed for the analysis.

m1 in more complex models as well, taking into account the effect of elevation and isolation.

Alien species

The number of alien species per island ranged from 0 to 7. Most of the alien species were introduced in historical times from mainland Europe, northern Africa and other areas of the Mediterranean basin. Only a few alien species, such as the North American slider turtle, *Trachemys scripta*, originated from different continents.

The geographical + human model was the best, according to AIC values, and explained a substantial proportion of variance ($R^2 = 0.496$). In this model, the number of alien species is highest on larger islands and on islands with airports (Table 2). The evidence ratio indicates that support for the geographical-only and of the human-only models is very low, since they were more than 1500 times less likely than the geographical + human model. We did not observe significant interactions between human and geographical factors.

Total number of species

Finally, to evaluate whether the increase in species richness caused by alien species compensates for the loss caused by

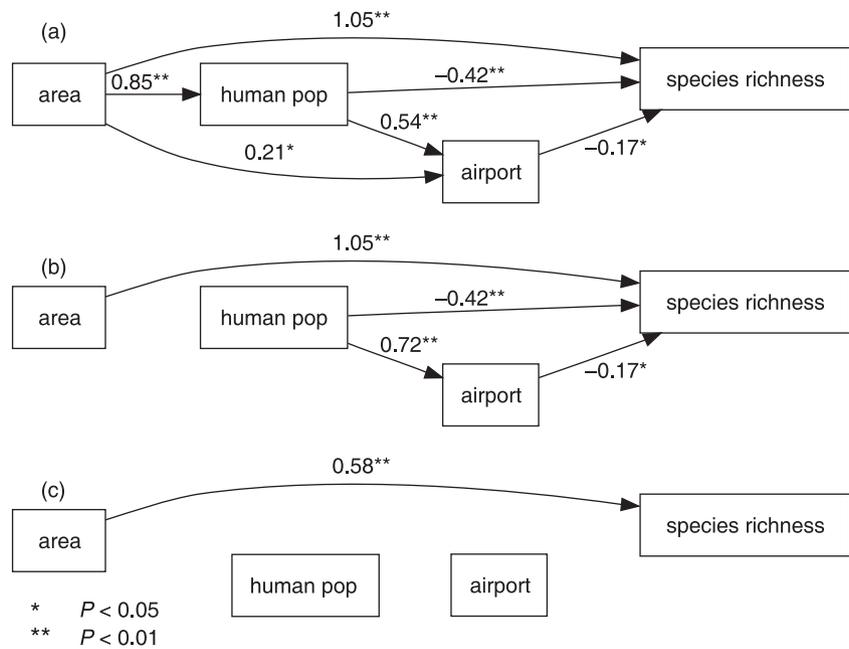


Figure 4 Path diagrams, representing three models of the relationships between island area, human population, presence of airports and richness of native reptiles. (a) Full model, assuming that island size affects species richness directly and through its relationship with human impact (model m1 in the Methods). (b) Both island size and human activities affect species richness, but there is no co-action among them (model m2). (c) Island size directly affects species richness, while human activities do not have an effect (m3). The model in (a) performed significantly better than the alternative models (see Results). The numerical values are the path coefficients.

human presence (Sax *et al.*, 2002), we built a model analysing total species richness, including both native and alien species. The total number of species per island ranged between 1 and 18. Once again, the best model included both human and geographical factors (Table 3). The total number of species was higher on large, high-elevation islands, and was lower on islands with a dense human population. This strongly suggests that an increase in alien species does not compensate for a decrease in species richness caused by human influence. Isolation and airport presence did not have a significant effect in this model, probably because they influenced native and alien species in opposite directions (see Tables 1 & 2). When we tested for interactions, we found a significant interaction between distance from the continent and human population ($F_{1,202} = 4.8, P = 0.03$), similar to the one observed for native species.

Similar to the model analysing native species, if anthropogenic factors were not included in the model, the relationship between $\log(\text{area})$ and $\log(\text{species richness})$ was not linear. A relationship with a break point fitted the data significantly better than a linear model ($F_{2,206} = 4.7, P = 0.01$), and its shape was similar to that estimated for native species (small islands, $z = 0.21, CI = 0.16-0.27$; large islands, $z = 0.10, CI = 0.06-0.15$). The estimated position of the break point was very close to that estimated for the data set including only native species (1.03 km^2), but the break point was not present if anthropogenic factors were included in the model. This further confirms that alien species do not compensate for the decrease in species richness related to human influence.

DISCUSSION

Our results show that human impact can strongly influence the pattern of island biogeography, and that it plays an important role in explaining the distribution of both native and alien species. Islands with high human impact host fewer native

Table 3 Regression models relating the overall richness of reptiles (natives + non-natives) to geographical and human factors.

	<i>b</i>	<i>F</i>	d.f.	<i>P</i>
Model: geographical-only				
$\Delta\text{AIC} = 23.4; w < 0.0001; R^2 = 0.580$				
Area*	0.13	87.2	1	< 0.001
Isolation*	-0.03	1.2	1	0.282
Elevation*	0.08	9.0	1	0.003
SEVM eigenvectors			2	
Residuals			206	
Model: human-only				
$\Delta\text{AIC} = 102.4, w < 0.0001, R^2 = 0.319$				
Human population*	0.08	24.6	1	< 0.001
Airport	0.08	0.8	1	0.372
SEVM eigenvectors			3	
Residuals			206	
Model: geographical + human				
$\Delta\text{AIC} = 0, w > 0.999, R^2 = 0.589$				
Area*	0.19	95.2	1	< 0.001
Isolation*	-0.04	2.8	1	0.095
Elevation*	0.11	15.2	1	< 0.001
Human population*	-0.06	12.1	1	< 0.001
Airport	-0.12	2.9	1	0.090
SEVM eigenvectors			3	
Residuals			203	

b, regression coefficients; ΔAIC , difference between a candidate model and the model with the lowest Akaike information criterion (AIC); *w*, AIC weight of the model; SEVM, spatial eigenvector mapping. *This variable was log-transformed for the analysis.

species than would be expected from a classical, linear biogeographical relationship, while they have an increased number of alien species. In other words, human impact seems to modify the biogeographical pattern, increasing the number of recent

colonizations (Blackburn *et al.*, 2008) and altering the pattern of extinction; thus it can displace island biodiversity from the equilibrium points expected on the basis of geographical features alone (MacArthur & Wilson, 1967). Path analysis provides insights into the complex mechanisms driving the richness of native species. On the one hand, island area has a positive, direct effect on reptile richness. On the other hand, large islands suffer the strongest human impact, which in turn negatively affects species richness (Fig. 4a). Therefore, human impact mediates an indirect negative relationship between island area and the richness of native reptiles.

Other studies have used smaller data sets to show that islands hosting large human populations have more alien species, most probably because on these islands aliens have higher risk of introduction and/or a lower probability of extinction after establishment (Chown *et al.*, 1998; Sax *et al.*, 2002; Blackburn *et al.*, 2008). Our analysis confirms that human population and exchanges are major factors explaining the distribution of alien species. However, an important role of natural processes in the establishment of introduced species cannot be ruled out (Table 2). After accounting for human influence, the largest islands still have more alien species, suggesting that island area increases the possibility of establishment of propagules (Chown *et al.*, 1998; Sax *et al.*, 2002; but see also Blackburn *et al.*, 2008).

However, human influence was not limited to an increase in the number of alien species, since the biogeographical relationship of native species seems to have been modified: inhabited islands had fewer native species than expected, assuming the usual species–area relationship. This was particularly evident on large islands (Fig. 3), which host the largest human populations. Other studies have found that the establishment of introduced species compensated for recent extinctions on islands, with no net change or even an increase of the overall species richness per island (Sax *et al.*, 2002). Conversely, the richness of Mediterranean reptiles was negatively related to human influence, even when native and alien species were summed (Table 3). This may indicate that insular reptiles may be particularly prone to extinction and/or that a smaller number of species has been introduced compared with other groups.

Recent extinctions of reptiles on Mediterranean islands are poorly documented due to the lack of fossil remains and the paucity of studies (e.g. Capula *et al.*, 2002), and the pattern of extinction can often be estimated only from indirect evidence (e.g. Foufopoulos & Ives, 1999). Nevertheless, on most islands, the currently ongoing decline of several species is clearly related to human influence. For instance, 67% of European terrestrial reptiles that are critically endangered by extinction are island endemics (IUCN, 2007). Several species are nearly extinct on the largest, human-inhabited islands because of human-induced factors such as alien species, predatory pets and pests (such as cats and rats) and habitat loss, and survive only in the smallest, uninhabited satellite islands (Capula *et al.*, 2002; Cox *et al.*, 2006; Pérez-Mellado *et al.*, 2008). Indeed, in temperate regions humans tend to settle in areas with the highest biodiversity (Stohlgren *et al.*, 2006); therefore, it is very unlikely that the reduced richness of reptiles in human-inhabited islands arises because

these islands naturally host a small number of native species. Despite the fact that we do not have direct data on historical extinctions, this reduced richness supports the idea that the smaller number of species on human-inhabited islands is probably due to a severe rise in the extinction rate.

An intense debate is ongoing in biogeography regarding the shape of species–area relationships. It has been proposed that natural ecological and geographical factors may affect the linearity of the relationships, yet evidence of deviation from a linear pattern (on log–log axes, i.e. a power law) is controversial (Lomolino, 2000, 2002; Williamson *et al.*, 2001). Some data sets suggest that the slope of the species–area relationship may decrease on large islands, and might even approach an asymptote (Lomolino, 2002; Kreft *et al.*, 2008). The strong relationship between human factors and species richness is probably widespread at the global scale, and we expect it to occur in other insular systems. Human influence may thus be an explanation of deviations from a simple linear pattern (e.g. Fig. 3). This hypothesis requires investigation across different groups and geographical areas, using data sets large enough to allow for testing of multiple hypotheses with enough statistical power.

Crutzen (2002) suggests that we are in a new geological era, the ‘Anthropocene’, in which humans are major drivers of global-scale processes, from atmospheric changes to biotic extinctions. Humans now rival natural geological and ecological processes in determining biodiversity at the global scale, and the present-day species distribution cannot be exhaustively analysed without considering human impact (Nogués-Bravo *et al.*, 2008). As macroecology becomes a vital tool in the study of global change (Kerr *et al.*, 2007), human influence should be integrated fully into biogeographical analyses for a more complete understanding of large-scale patterns and processes.

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REFERENCES

- Anonymous (2003) *Etude des plans de gestion des sites MEDWET-COAST – site de Zembra*. Coastal Protection and Planning Agency, Ministry of Environment, Republic of Tunisia.
- Blackburn, T.M., Cassey, P., Duncan, R.P., Evans, K.L. & Gaston, K.J. (2004) Avian extinction and mammalian introductions on oceanic islands. *Science*, **305**, 1955–1958.
- Blackburn, T.M., Cassey, P. & Lockwood, J.L. (2008) The island biogeography of exotic bird species. *Global Ecology and Biogeography*, **17**, 246–251.
- Blondel, J. & Aronson, J. (1999) *Biology and wildlife of the Mediterranean region*. Oxford University Press, New York.
- Bollen, K.A. & Long, J.S. (1993) *Testing structural equation models*. Sage, Newbury Park, CA.

- Bowerman, B.L. & O'Connell, R.T. (1990) *Linear statistical models*. PWS-Kent, Boston.
- Bryman, A. & Cramer, D. (1990) *Quantitative data analysis for social scientists*. Routledge, London.
- Buckley, L.B. & Jetz, W. (2007) Insularity and the determinants of lizard population density. *Ecology Letters*, **10**, 481–489.
- Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodel inference: a practical information-theoretic approach*. Springer Verlag, New York.
- Capula, M., Luiselli, L., Bologna, M.A. & Ceccarelli, A. (2002) The decline of the Aeolian wall lizard, *Podarcis raffonei*: causes and conservation proposals. *Oryx*, **36**, 66–72.
- Castanet, J. & Guyétant, R. (1989) *Atlas de répartition des amphibiens et reptiles de France*. Société Herpétologique de France, Paris.
- Chown, S.L., Gremmen, N.J.M. & Gaston, K.J. (1998) Ecological biogeography of southern ocean islands: species-area relationships, human impacts, and conservation. *The American Naturalist*, **152**, 562–575.
- Cox, N., Chanson, J.S. & Stuart, S.N. (2006) *The status and distribution of reptiles and amphibians of the Mediterranean basin*. IUCN, Gland, Switzerland.
- Crutzen, P.J. (2002) Geology of mankind. *Nature*, **415**, 23.
- Daget, P. (1977) Le bioclimat méditerranéen: caractères généraux, modes de caractérisation. *Vegetatio*, **34**, 1–20.
- Delaguerre, M. & Cheylan, M. (1992) *Atlas de répartition des batraciens et reptiles de Corse*. Parc Naturel Régional de Corse-Ecole Pratique de Hautes Etudes, Pampelune.
- Diamond, J.M. (1969) Avifaunal equilibria and species turnover rates on the Channel Islands of California. *Proceedings of the National Academy of Sciences USA*, **64**, 57–63.
- Dormann, C.F. (2007) Effects of incorporating spatial autocorrelation into the analysis of species distribution data. *Global Ecology and Biogeography*, **16**, 129–138.
- Dormann, C.F., McPherson, J.M., Araújo, M.B., Bivand, R., Bolliger, J., Carl, G., Davies, R.G., Hirzel, A., Jetz, W., Kissling, W.D., Kühn, I., Ohlemüller, R., Peres-Neto, P.R., Reineking, B., Schröder, B., Schurr, F.M. & Wilson, R. (2007) Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography*, **30**, 609–628.
- Foufopoulos, J. & Ives, A.R. (1999) Reptile extinctions on land-bridge islands: life-history attributes and vulnerability to extinction. *The American Naturalist*, **153**, 1–25.
- Griffith, D.A. & Peres-Neto, P.R. (2006) Spatial modelling in ecology: the flexibility of eigenfunction spatial analyses. *Ecology*, **87**, 2603–2613.
- IUCN (2007) *2007 IUCN red list of threatened species*. <http://www.iucnredlist.org/> (accessed 15 February 2008).
- Kadmon, R. & Allouche, O. (2007) Integrating the effects of area, isolation, and habitat heterogeneity on species diversity: a unification of island biogeography and niche theory. *The American Naturalist*, **170**, 443–454.
- Kalmar, A. & Currie, D.J. (2006) A global model for island biogeography. *Global Ecology and Biogeography*, **15**, 72–81.
- Kerr, J.T., Kharouba, H.M. & Currie, D.J. (2007) The macroecological contribution to global change solutions. *Science*, **316**, 1581–1584.
- Kreft, H., Jetz, W., Mutke, J., Kier, G. & Barthlott, W. (2008) Global diversity of island floras from a macroecological perspective. *Ecology Letters*, **11**, 116–127.
- Lanza, B. & Poggesi, M. (1986) *Storia naturale delle isole satelliti della Corsica*. Istituto Geografico Militare, Firenze.
- Lever, C. (2003) *Naturalized amphibians and reptiles of the world*. Oxford University Press, New York.
- Lomolino, M.V. (2000) Ecology's most general, yet protean pattern: the species-area relationship. *Journal of Biogeography*, **27**, 17–26.
- Lomolino, M.V. (2002) '... there are areas too small, and areas too large, to show clear diversity patterns ...' R.H. MacArthur (1972: 191). *Journal of Biogeography*, **29**, 555–557.
- MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography*. Princeton University Press, Princeton, NJ.
- Malkmus, R. (2004) *The amphibians and reptiles of Portugal, Madeira and the Azores archipelago*. Koeltz Scientific Books, Koenigstein.
- Muggeo, V.M.R. (2003) Estimating regression models with unknown break-points. *Statistics in Medicine*, **22**, 3055–3071.
- Nogués-Bravo, D., Araújo, M.B., Romdal, T. & Rahbek, C. (2008) Scale effects and human impact on the elevational species richness gradients. *Nature*, **453**, 216–219.
- Pérez-Mellado, V., Hernández-Estévez, J.A., García-Díez, T., Terrassa, B., Ramón, M.M., Castro, J., Picornell, A., Martín-Vallejo, J. & Brown, R. (2008) Population density in *Podarcis lilfordi* (Squamata, Lacertidae), a lizard species endemic to small islets in the Balearic Islands (Spain). *Amphibia-Reptilia*, **29**, 49–60.
- Pleguezuelos, J.M., Márquez, R. & Lizana, M. (2002) *Atlas y libro rojo de los Anfibios y Reptiles de España*. Dirección General de Conservación de la Naturaleza-Asociación Herpetológica Española, Madrid.
- R Development Core Team (2007) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna (<http://www.r-project.org/>).
- Rangel, T.F.L.V.B., Diniz-Filho, J.A.F. & Bini, L.M. (2006) Towards an integrated computational tool for spatial analysis in macroecology and biogeography. *Global Ecology and Biogeography*, **15**, 321–327.
- Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M. & Wall, D.H. (2000) Biodiversity – global biodiversity scenarios for the year 2100. *Science*, **287**, 1770–1774.
- Sax, D.F., Gaines, S.D. & Brown, J.H. (2002) Species invasions exceed extinctions on islands worldwide: a comparative study of plants and birds. *The American Naturalist*, **160**, 766–783.
- Sindaco, R., Doria, G., Razzetti, E. & Bernini, F. (2006) *Atlas of Italian amphibians and reptiles*. Polistampa, Firenze.
- Steadman, D.W. (1993) Biogeography of Tongan birds before and after human impact. *Proceedings of the National Academy of Sciences USA*, **90**, 818–822.
- Stohlgren, T.J., Barnett, D.T., Flather, C., Fuller, P., Peterjohn, B., Kartesz, J.T. & Master, L.L. (2006) Species richness and pattern

- of invasion in plants, birds, and fishes in the United States. *Biological Invasions*, **8**, 427–447.
- Sultana, J. & Falzon, V. (2002) *Wildlife of the Maltese islands*. BirdLife Malta, Malta.
- Toms, J.D. & Lesperance, M.L. (2003) Piecewise regression: a tool for identifying ecological thresholds. *Ecology*, **84**, 2034–2041.
- Whittaker, R.J. (1995) Disturbed island ecology. *Trends in Ecology and Evolution*, **10**, 421–425.
- Whittaker, R.J. & Fernández-Palacios, J.M. (2007) *Island biogeography*. Oxford University Press, Oxford.
- Williamson, M., Gaston, K.J. & Lonsdale, W.M. (2001) The species–area relationship does not have an asymptote! *Journal of Biogeography*, **28**, 827–830.
- Wilson, E.O. (2002) *The future of life*. Little Brown, London.
- Wright, D.H. (1983) Species–energy theory: an extension of species–area theory. *Oikos*, **41**, 496–506.

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